Shell Selection and Invasion Rates of Some Pacific Hermit Crabs

Gordon H. Orians and Charles E. King[1]

ABSTRACT: Three species of littoral hermit crabs from Horseshoe Cove, Bodega Head, Sonoma County, California, and three sublittoral pagurids from Chinimi Island, Eniwetok Atoll, Marshall Islands, have been examined with respect to their shell selection and invasion rates.

Periodic removal of crabs from marked areas resulted in immigrations of surprising magnitude. By comparison of actual collection patterns with those predictable from the alternates of density dependence and density independence, there is an indication that the observed immigration rates result from density-dependent dispersal. While our data are not conclusive, the method presented is of interest and of possible utility for examining problems of this nature.

Shell selection is discussed from the bases of both laboratory and field observations. Each of the species is shown to utilize the shells of different gastropods with different frequencies.

Finally, behavioral aspects are examined as they relate to the distribution of the California hermit crabs.

SHELLS of various species of gastropod molluscs constitute a necessary component in the environment of pagurid crabs. In addition to housing the crab the shell may act as an important determinant of behavior; for instance, several species will not feed unless in a shell (Allee and Douglis, 1945; Brightwell, 1952). Different species of pagurids regularly utilize different species of shells and it has been suggested that shell availability may be a limiting factor for some species (Provenzano, 1960).

This paper reports on observations of shell utilization by six species of Pacific hermit crabs and on some simple laboratory experiments on shell selection. In addition, a number of removal and repopulation experiments were performed. Orians worked mainly at Horseshoe Cove, Bodega Head, Sonoma County, California, during the summer of 1957, and King at Chinimi Island of Eniwetok Atoll during the summer of 1961.

The study area at Horseshoe Cove consisted of a section of rocky, shelving shore partially protected from heavy ocean swell, with an abundance of small tidal pools at high and medium intertidal ranges. Twenty-seven pools in the tidal range 2.5–4.5 ft above datum (which is mean low water) and subjected to long periods of exposure at low tides, were selected because they were easily reached at most tides. They ranged in length from 0.43 to 9.5 m and in depth from 15 cm to approximately 1 m. Plant cover varied from virtually nothing to dense algal growth covering the bottoms and sides of the pools. During the period of study, temperatures never rose above 17 C in the lower and deeper pools but on warm, sunny afternoons temperatures rose to as high as 27 C in some of the higher, shallower pools. However, no correlation was found between pagurid distribution and maximum pool temperature. Three species of hermit crabs found on this study area were *Pagurus hirsutiusculus, P. samuelis,* and *P. granosimanus.*

The site of King's study was approximately 100 m offshore in the lagoon adjacent to Chinimi Island of Eniwetok Atoll. At this location the depth is 7 m and the substrate is uniformly composed of coralline sand mixed with fine pieces of dead coral. A 256 m² area was divided with a thin cord into 16 squares of 16 m² each. These squares were designated by letters from
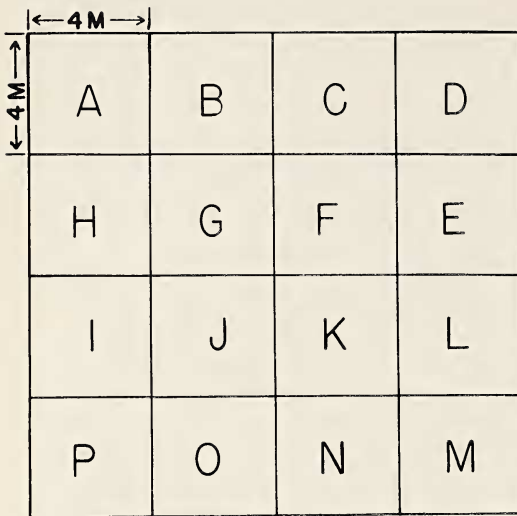
FIG. 1. Sampling grid, Eniwetok Atoll.

A to P as depicted in Figure 1. Three people participated in each of the four collections of these quadrats. One person started at Square A and collected in alphabetical order areas A to P while a second started at Square P and collected in reverse order P to A. The third person, after distributing labeled jars to each square, searched the area a third time. The majority of the pagurids were obtained the first time the square was examined, although two or three individuals were usually found in the second examination. Hermit crabs were rarely obtained by the third collector. Using double-block aqua-lung tanks, it was feasible to collect continuously and minimize pagurid movement into the area during the collecting process. The entire procedure required 1.5–2 hr to clear the 256 m² area of essentially all pagurids, gastropods, and empty

gastropod shells. Collections were made, starting around noon, on July 10, 1961 (collection no. F-2), July 22, 1961 (F-3), July 29, 1961 (F-4), and August 7, 1961 (F-5). Three species of hermit crabs occurred consistently in most squares of each sample at Eniwetok: *Diogenes gardineri, Dardanus scutellatus,* and *Calcinus latens.* Their abundances (expressed as mean number/square) are presented in Table 1.

Appreciation is expressed to Anthony J. Provenzano, Jr., who identified the Eniwetok pagurids, and to David Au, David Fellows, John Shoup, and Stanley Swerdloff for their aid in making the Eniwetok collections. Ernst Reese and R. T. Paine offered many valuable comments during the preparation of the manuscript.

INVASION RATES

At Horseshoe Cove all of the crabs of the most abundant species were removed at weekly intervals from two pools in which *P. samuelis* was the most abundant pagurid and from one pool in which the most abundant species was *P. hirsutiusculus.* The results are indicated in Figure 2D. Whereas populations of the most abundant crab were definitely reduced by the removals, the influx was of surprising magnitude, resulting in a total removal from the pools in a 3-week period of over twice the number of crabs initially present in one case. Crabs from the pool in which *P. hirsutiusculus* was most abundant were removed only once due to tidal conditions, but in this pool the final population of *P. hirsutiusculus* was larger than the initial one.

Since the time interval between collections was not constant, it is difficult to compare the rates of invasion after successive samples. A

TABLE 1

MEAN NUMBER OF PAGURIDS PER SQUARE FOR EACH SPECIES IN ALL ENIWETOK SAMPLES

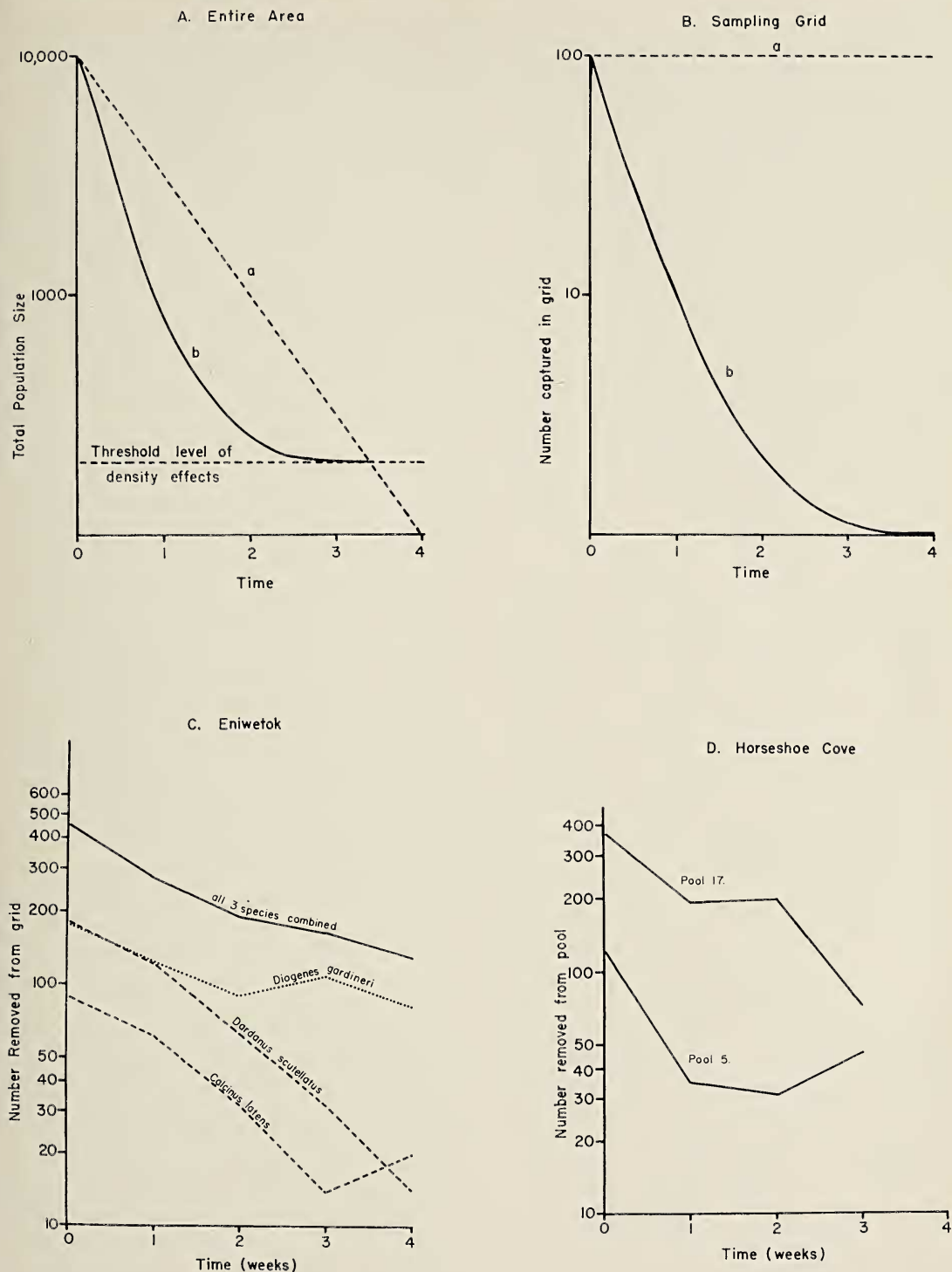| SAMPLE | DATE | MEAN NUMBER PAGURIDS/SQUARE | | | TOTALS |
		Diogenes gardineri	*Dardanus scutellatus*	*Calcinus latens*	
F–2	10 July	11.2	11.4	5.5	28.1
F–3	22 July	4.9	4.4	2.3	11.6
F–4	29 July	7.1	2.3	0.8	10.2
F–5	7 Aug.	4.9	1.9	1.2	8.0

FIG. 2. Predicted and observed dispersal rates. *A*, Predicted rates of dispersal. Curve *a*—if dispersal is density independent. Curve *b*—if dispersal is density dependent. *B*, Predicted numbers of individuals entering the sampling grid. Curve *a*—if dispersal is density independent. Curve *b*—if dispersal is density dependent. *C*, Observed numbers of individuals entering Eniwetok sampling grid. *D*, Observed numbers of individuals entering pools at Horseshoe Cove.

rough, but, for the purposes of the present paper, adequate method of obtaining comparable data is to extrapolate from the original curve plotted from the data in Table 1. This has been done in Figure 2C, with the original curve being evaluated at 7-day intervals.

Andrewartha and Birch (1954) have discussed the innate tendency of animals to disperse, but apparently they attached little general significance to dispersal in response to crowding. Such a mechanism has been shown for the great tit by Kluijver (1951) and it is known that in some crab species dispersal is directly related to population density (Bovbjerg, 1960). It is obvious from Figures 2C and 2D that there are strong dispersal movements into the unoccupied area within a relatively brief period. It is not obvious, however, whether this dispersal is in response to the density of the individuals outside the sampling area. To examine this problem, two alternates may be erected:

Alternate 1: Dispersion remaining constant and independent of density. Assuming that the dispersion of pagurid populations is constant and independent of their density, all crabs would spend a great deal of their time wandering about. If the individuals found in a grid, such as that erected at Eniwetok, were removed at constant intervals, the total size of the pagurid populations would decrease at a constant rate, as is hypothetically depicted in Figure 2A (curve a). This pattern assumes both density independence and a *status quo,* with no death or recruitment to the population. Viewed from the number of individuals collected in the grid, however, a different pattern would result from the same assumptions. Since the total size of the pagurid populations is very large, compared to those collected in the grid, the number of individuals collected at each interval would not vary to any great extent. The result (Fig. 2B, curve a) would be a curve which was parallel to the abscissa or which decreased linearly to a very slight extent. Continued for an extremely long time, the curve would approach that obtained by viewing the entire area, since every crab would eventually wander across the grid. When crabs ceased to enter the grid, the explanation required by density-independent dispersal is that all crabs have been collected.

Alternate 2: Dispersion as a function of den-

sity. Assuming that the tendency to disperse increases with increasing population size and conversely decreases with decreasing population size, a different pattern would result. The number of pagurids in the entire area (Fig. 2A, curve b) would initially drop at a rate greater than the final rate. The curve then indicates a variable rather than a constant-rate function. At the threshold of density-dependent dispersal effects, that is, at the point above which crabs disperse and below which they do not, the number of crabs obtained in the sampling grid (Fig. 2B, curve b) would be 0. However, in contrast to density-independent dispersal, there would still be pagurids in the area (as depicted in Fig. 2A, curve b).

A final evaluation of these two alternates is not possible in the present study. For example, surf action may be responsible for most of the influx at Horseshoe Cove, and no marking and recapture experiments were made at either site. However, there are indications that Alternate 2 more adequately explains the data. If the immigration rates of the three Eniwetok crabs are examined, either lumped or separately (Fig. 2C), it is apparent that the pattern more nearly approximates that required for density-dependent dispersal than it does for density-independent dispersal (Fig. 2B). Variations in the slopes of the collecting patterns may possibly reflect differences in the initial density levels relative to the threshold of density effects.

Repopulation of two Horseshoe Cove pools (Fig. 2D) also agrees more closely with Alternate 2 than with Alternate 1.

SHELL UTILIZATION

Shells housing individual pagurids were identified whenever possible. Each pagurid species was found to utilize the shells of different gastropods with different frequencies in both the Eniwetok and Californian studies (Tables 2 and 3).

To test for homogeneity of shell utilization in various samples of the same species and to inspect the collections for interspecific differences in shell utilization, a trellis diagram was constructed (Fig. 3). For a discussion of the mechanics of this type of test, the reader is referred to Wieser (1960) and Sanders (1960).

TABLE 2

SHELL UTILIZATION BY HERMIT CRABS AT HORSESHOE COVE, CALIFORNIA

SHELL SPECIES	P. hirsutiusculus		P. samuelis		P. granosimanus	
	No.	%	No.	%	No.	%
Thais emarginata	271	50.9	48	3.9	44	21.6
Tegula brunnea	18	3.4	116	9.5	49	24.0
Tegula funebralis	53	10.0	722	59.0	37	18.1
Calliostoma costatum	53	10.0	297	24.3	13	6.4
Littorina planaxis	72	13.5	18	1.5	2	1.0
Other	65	12.2	22	1.8	59	28.9
Total	532		1223		204	

All samples of *Diogenes gardineri* are uniform in their shell utilization, that is, the overlap in shells used is greater than 60% in each case. Similarly, *Dardanus scutellatus* is homogeneous when compared with itself. The trellis diagram indicates that sample F-4 of *Calcinus latens* differs from all other samples of the same species, but no significance may be attached to it, since only four individuals of this species were obtained in sample F-4.

There is very little overlap ($< 30\%$) in the species of shells utilized by *Diogenes gardineri* and *Dardanus scutellatus*. With the exception of the F-4 sample of *Calcinus latens* discussed above, there is little overlap between *Dardanus scutellatus* and *Calcinus latens*, but the similarity is greater than between *Diogenes gardineri* and *Dardanus scutellatus*.

It is evident from the diagram that *Diogenes gardineri* and *Calcinus latens* are very similar in their shell requirements ($> 60\%$ overlap, with the exception of the F-4 sample of *Calcinus latens*), even though different samples of the shells utilized by *Diogenes gardineri* resemble each other, and different shell samples of *Calcinus latens* resemble each other more than the samples of *Diogenes gardineri* resemble samples of *Calcinus latens*.

The overlap in the Californian samples between *Pagurus hirsutiusculus* and *P. samuelis* was 30%; between *P. hirsutiusculus* and *P. granosimanus*, 46%; between *P. samuelis* and *P. granosimanus*, 40%.

Shell utilization is basically dependent upon the availability of shells and the morphological limitations of the individual hermit crab. Thus the shells which are available, and hence utilized,

by *Pagurus samuelis* in northern California as determined in the present study, are markedly different from those utilized by the same species in southern California (Coffin, 1954). Similarly, it is not to be inferred that the differences in shell utilization of the three Eniwetok pagurids are due to preferences of the species. The distinct differences may be explained on the simpler basis of differences in crab size. *Dardanus scutellatus*, which differs most markedly from the other two species in shell utilization, is also markedly larger (with average wet weight of 0.81 g) than both *Calcinus latens* (0.07 g) and *Diogenes gardineri* (0.04 g). As might be expected, *Calcinus latens* and *Diogenes gardineri*, which are similar in shell utilization, are also similar in size.

Shells may also be selected as a function of species-specific preferences and social interactions as discussed in the next section, but data of this type are not available for the Eniwetok hermit crabs.

EXPERIMENTS

To test the possibility of active shell selection, crabs were taken from Horseshoe Cove and subjected to the following types of experiments in the laboratory: (1) A single crab was given a choice of several shells of different species; (2) crabs of two or more species were presented with a single unoccupied shell.

Experimental crabs were removed from their shells by the application of a lighted match to the posterior portion of the shell. When the crab relinquished its hold it was placed in a shallow petri dish with the unoccupied shells. *Pagurus hirsutiusculus* consistently preferred

TABLE 3

SHELL UTILIZATION BY HERMIT CRABS AT ENIWETOK

GASTROPOD SHELL	Diogenes gardineri						Dardanus scutellatus						Calcinus latens					
	F-2	F-3	F-4	F-5	Total No.	Total %	F-2	F-3	F-4	F-5	Total No.	Total %	F-2	F-3	F-4	F-5	Total No.	Total %
Strombus gibberulus	11	3	1	—	15	5.8	21	2	7	3	33	14.1	15	3	2	—	20	17.9
Strombus mutabilis	2	—	—	—	2	0.8	—	—	—	—	—	—	—	—	1	1	1	0.9
Strombus luhuanus	1	—	—	—	1	0.4	63	16	12	6	97	41.5	6	1	1	—	9	8.0
Strombus tips	54	17	31	49	151	58.0	8	2	3	4	17	7.3	45	15	—	12	72	64.2
Terebra striata	6	1	3	1	11	4.1	—	—	—	—	—	—	1	—	—	—	1	0.9
Terebra crenulata	—	—	—	—	—	—	1	—	—	—	1	0.4	—	—	—	—	—	—
Terebra maculata	—	—	—	—	—	—	53	7	6	5	71	30.4	—	—	—	—	—	—
Cerithium sp.	10	1	5	5	21	8.1	—	—	—	—	—	—	—	1	1	1	2	1.8
Mitra sp.	15	2	4	3	24	9.4	—	—	—	—	—	—	—	1	—	—	1	0.9
Mitra olivaeformis	—	—	1	1	2	0.8	—	—	—	—	—	—	—	—	—	—	—	—
Mitridae	—	6	1	3	10	3.8	—	—	—	—	—	—	1	—	—	1	2	1.8
Cymatiidae	1	—	—	—	1	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Cymatium muricinum	—	—	—	—	—	—	—	—	—	1	1	0.4	—	—	—	—	—	—
Natica onca	3	2	—	2	7	2.7	—	—	—	—	—	—	—	—	—	2	2	1.8
Conus sponsalis	1	—	—	—	1	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Conus consors	—	—	—	—	—	—	1	—	—	—	1	0.4	—	—	—	—	—	—
Conus eburneus	—	—	—	—	—	—	1	1	—	—	2	0.9	2	—	—	—	2	1.8
Conus pulicarius	—	—	—	—	—	—	3	—	1	—	4	1.7	—	—	—	—	—	—
Vexillum exasperata	1	2	3	5	11	4.1	—	—	—	—	—	—	—	—	—	—	—	—
Morula elata	1	—	1	—	1	0.4	3	—	—	—	3	1.3	—	—	—	—	—	—
Drupa morum	—	—	—	—	—	—	1	—	—	—	1	0.4	—	—	—	—	—	—
Latirus barclav	—	—	—	—	—	—	1	—	1	—	1	0.4	—	—	—	—	—	—
Thais sp.	—	—	—	—	—	—	—	—	1	—	1	0.4	—	—	—	—	—	—
Trochus niloticus	—	—	1	—	1	—	—	—	1	—	1	0.4	—	—	—	—	—	—
Rhinoclavis sinensis	—	—	—	1	1	0.4	—	—	—	—	—	—	—	—	—	—	—	—
Totals	106	34	50	70	260	100	156	28	31	19	234	100	70	20	4	18	112	100

shells of *Thais emarginata,* leaving shells of *Tegula* and *Calliostoma* for *Thais* even when the latter were so small as to preclude the withdrawing of the carapace into the shell. Never did a crab leave a *Thais* for shells of the other two species, and in every case in which crabs were forced to use *Tegula* and *Calliostoma* they left them as soon as a *Thais* was again made available. *P. samuelis* and *P. granosimanus,* on the other hand, showed no preference between shells of *Tegula funebralis, T. brunnea,* and *Calliostoma costatum* as long as the shell was of proper size. A marked preference for shells of *Tegula* was noted for *P. samuelis* in southern California by Coffin (1954). However, adult *P. granosimanus* were so large that only *Tegula*

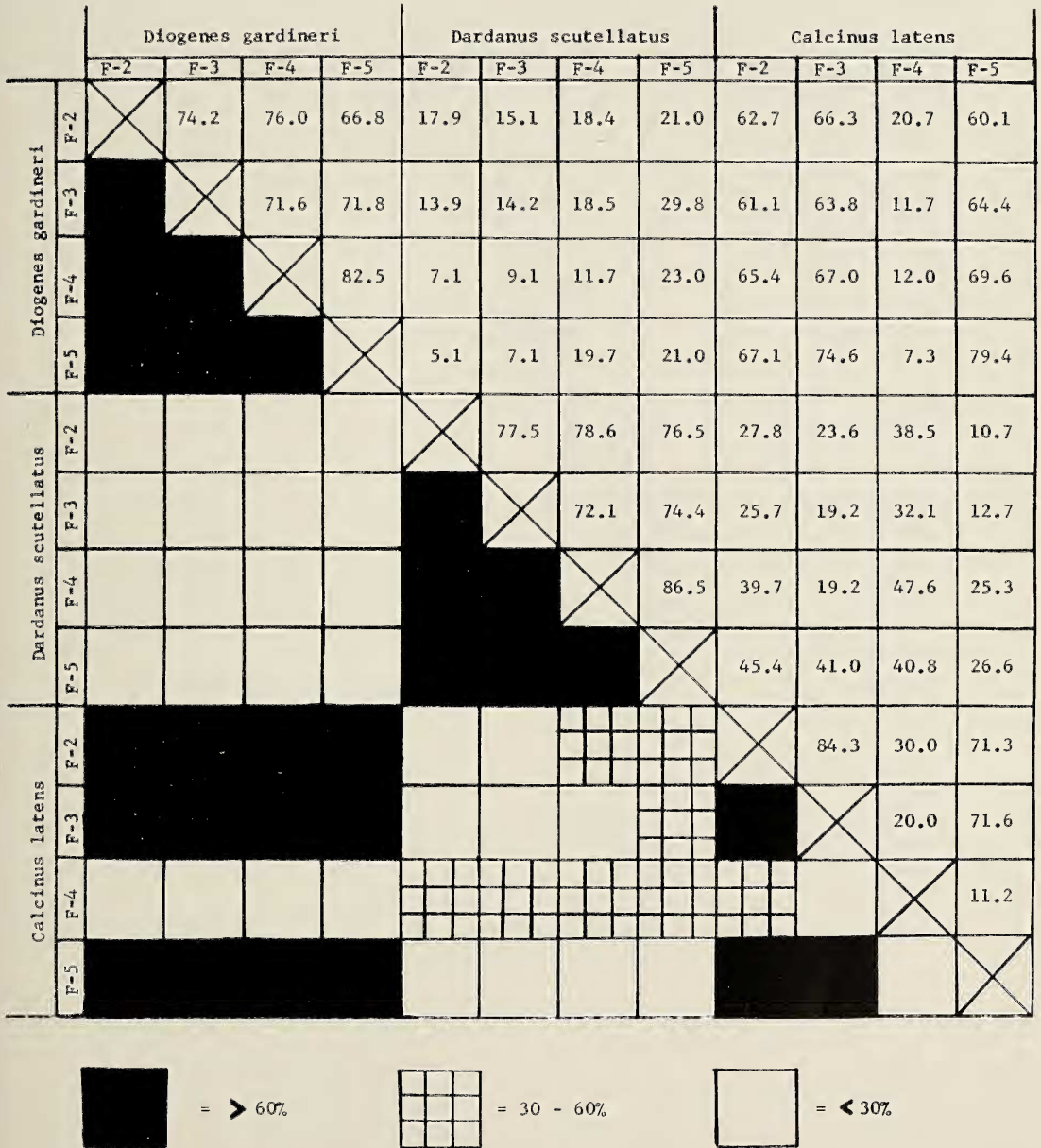|		Diogenes gardineri				Dardanus scutellatus				Calcinus latens			
		F-2	F-3	F-4	F-5	F-2	F-3	F-4	F-5	F-2	F-3	F-4	F-5
Diogenes gardineri	F-2	✕	74.2	76.0	66.8	17.9	15.1	18.4	21.0	62.7	66.3	20.7	60.1
	F-3	■	✕	71.6	71.8	13.9	14.2	18.5	29.8	61.1	63.8	11.7	64.4
	F-4	■	■	✕	82.5	7.1	9.1	11.7	23.0	65.4	67.0	12.0	69.6
	F-5	■	■	■	✕	5.1	7.1	19.7	21.0	67.1	74.6	7.3	79.4
Dardanus scutellatus	F-2					✕	77.5	78.6	76.5	27.8	23.6	38.5	10.7
	F-3					■	✕	72.1	74.4	25.7	19.2	32.1	12.7
	F-4					■	■	✕	86.5	39.7	19.2	47.6	25.3
	F-5					■	■	■	✕	45.4	41.0	40.8	26.6
Calcinus latens	F-2	■	■	■	■			▦	▦	✕	84.3	30.0	71.3
	F-3	■	■	■	■			▦	▦	■	✕	20.0	71.6
	F-4	■			■	▦	▦	▦	▦	■	■	✕	11.2
	F-5	■	■	■	■				■	■	■	■	✕

■ = > 60% ▦ = 30 - 60% ☐ = < 30%

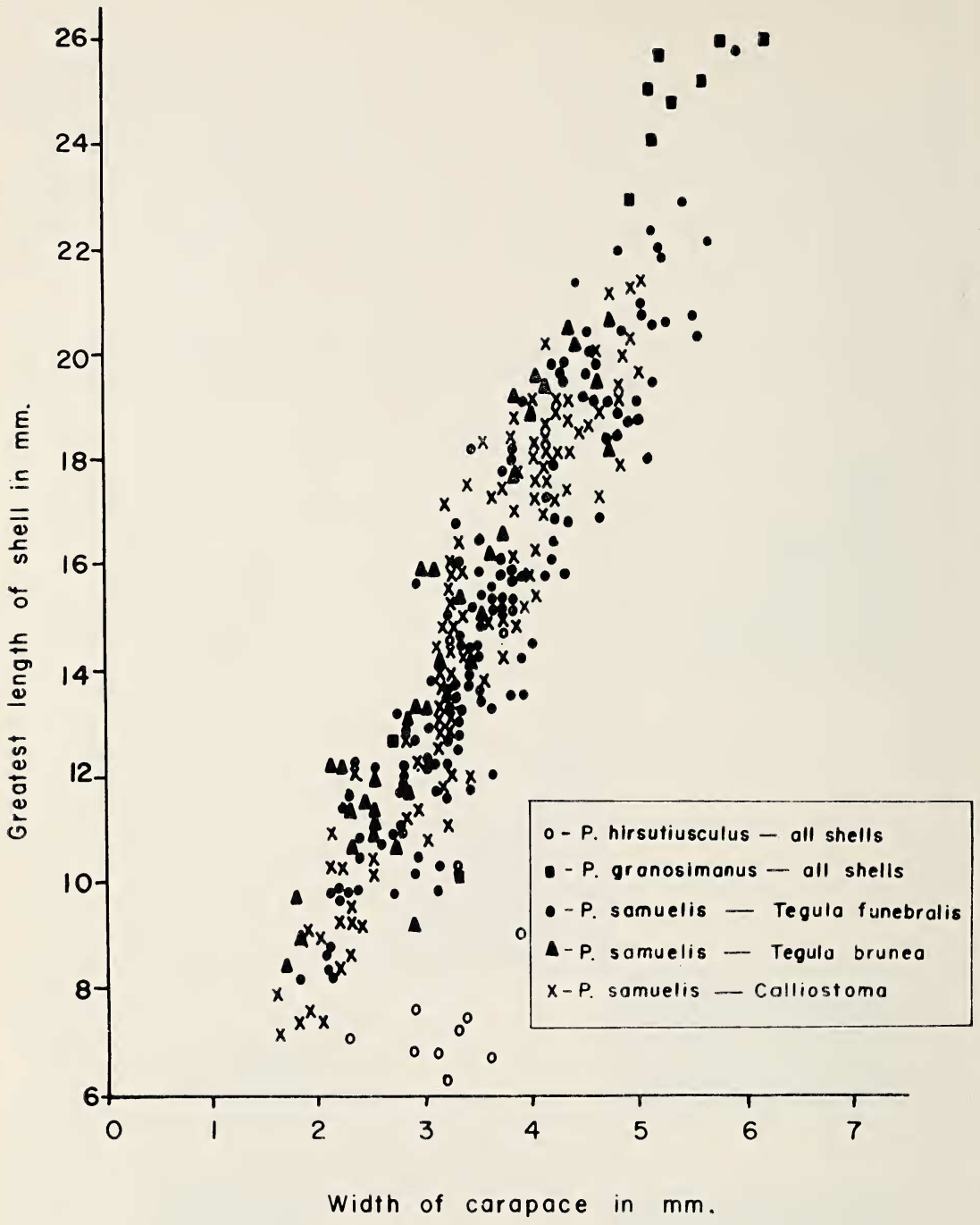FIG. 3. Trellis diagram showing overlap in shell utilization in four samples of Eniwetok pagurids.

FIG. 4. Relationship between size of shell utilized and size of crab at Horseshoe Cove.

brunnea shells were of suitable size and they consequently were preferred. Both of these species chose shells of a size to permit the entire carapace to be withdrawn until the large cheliped was in a position to act as an operculum. This preference is reflected in the size of shells utilized by the crabs in nature (Fig. 4).

In eviction experiments, *P. hirsutiusculus* was dominated by the other two species, usually being evicted by crabs of the other species if they made such an attempt. In no case did a specimen of *P. hirsutiusculus* successfully evict

a crab of the other two species from a shell, even when it had a decided size advantage. Immunity from eviction was conferred only when a *P. hirsutiusculus* was in a *Thais* shell too small to interest the other crabs. No clear dominance was found between *P. samuelis* and *P. granosimanus*. Size appeared to be the critical factor in outcomes, but more experiments are needed to confirm this tentative conclusion. Interspecific dominance in hermit crabs in which species membership is more important than size has also been reported by Reese (1961).

In attempting to evict a crab from its shell, invaders of all three species follow a general behavior pattern. A crab without a shell or with an unsuitable shell, upon making contact with a shell, immediately tests the size of the shell with its chelipeds and quickly moves into a position where it is able to probe the aperture. Eviction of a crab already occupying the shell is effected by grasping either the legs or the antenna with the large cheliped and smoothly sliding the occupant from the shell. Then while holding the evicted individual at arm's length, the intruder slides out of its own shell, if it has one, and into the newly vacated shell. During the probing, shell-less crabs frequently twitch their abdomens violently.

It is interesting that a human is unable to pull either of the larger species from their shells with forceps without severely injuring the animals and yet an intruding crab is able to do so with ease (see also Allee and Douglis, 1945; Brightwell, 1952). One must therefore conclude that the evicted crab releases its hold and, though there are no data to test this, it is possible that the striking difference in behavior has important survival value. A larger crab may be able to exert enough force to sever the cheliped from the body or otherwise injure the inhabitant. If evicted, however, another shell may be found and the probability of survival increased. In contrast, if the attack is by a large predator, eviction probably means certain death, so that chances of surviving would be enhanced by remaining in the shell at all costs.

SIGNIFICANCE OF SHELL SELECTION

It is possible to observe a relationship between the types of shells selected and the habitat utilized by the crabs in California. *Pagurus hirsutiusculus*, which under laboratory conditions prefers smaller shells, is much more mobile than the other two species and is able to climb over the algal growth in the pools better than the other species. Both *P. samuelis* and *P. granosimanus*, with their heavier shells, restrict their activities to the bottoms of the pools. This may be explained either by comparative ability to climb as related to shell weight or as the result of the aggressive dominance of *P. samuelis* and *P. granosimanus* over *P. hirsutiusculus* which was discussed earlier. Thus, though *P. hirsutiusculus* and *P. samuelis* are found together in most of the tidal pools in Horseshoe Cove, their distribution within the pools differs significantly as tested by the Fisher Exact Probability Test (Siegel, 1956). *P. hirsutiusculus* was the most common pagurid in 11 pools with good algal growth, but was the most abundant species in only 3 pools with poor algal growth. In contrast, *P. samuelis* was most common in 9 pools with few plants, but was the most abundant crab in only 2 pools with good algal growth (Table 4). Coffin (1954) also noted the importance of rocky bottoms in tidal pools containing *P. samuelis* and was able to greatly reduce crab population densities by removing rocks.

From the results of the survey of shell utilization in natural populations of hermit crabs, supported by the results of shell selection experiments, it can be concluded that not only is there active shell selection by hermit crabs which differs from species to species, but also

TABLE 4

HERMIT CRAB ABUNDANCE AND TIDAL POOL CONDITIONS AT HORSESHOE COVE, CALIFORNIA

NATURE OF POOL	NUMBER OF POOLS IN WHICH THE MOST ABUNDANT HERMIT CRAB WAS		P
	Pagurus hirsutiusculus	*Pagurus samuelis*	
Good to dense algal growth	11	2	
Plants few and scattered	3	9	.01
Sandy bottom	3	1	insig.
Rocky bottom	9	7	

that this can be correlated with what little is known of the habits of these animals.

REFERENCES

ALLEE, W. C., and M. B. DOUGLIS. 1945. A dominance order in the hermit crab, *Pagurus longicarpus* Say. Ecology 26:411–412.

ANDREWARTHA, H. G., and L. C. BIRCH. 1954. The Distribution and Abundance of Animals. Univ. of Chicago Press.

BOVBJERG, R. V. 1960. Behavioral ecology of the crab, *Pachygrapsus crassipes*. Ecology 41: 668–672.

BRIGHTWELL, L. K. 1952. Some experiments with common hermit crab (*Eupagurus bernhardus*) Linn., and transparent univalve shells. Proc. Zool. Soc. Lond. 121:279–283.

COFFIN, H. G. 1954. The biology of *Pagurus samuelis* (Stimpson). Unpublished thesis. Univ. of Southern California.

KLUIJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea 39:1–135.

PROVENZANO, A. J., JR. 1960. Notes on Bermuda hermit crabs (Crustacea; Anomura). Bull. Mar. Sci. Gulf and Caribbean 10:117–124.

REESE, E. S. 1961. Inter- and intraspecific dominance relationships of sympatric species of intertidal hermit crabs. Amer. Zoologist 1:60.

SANDERS, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft bottom community. Limnol. Oceanog. 5:138–153.

SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, N. Y.

WIESER, W. 1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanog. 5: 121–137.